Selective attention to stimulus location modulates the steady-state visual evoked potential

(electroencephalogram/electrophysiology/electrophysiology/Fourier/spatial cuing)

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ABSTRACT Steady-state visual evoked potentials (SS-VEPs) were recorded from the scalp of human subjects who were cued to attend to a rapid sequence of alphanumeric characters presented to one visual half-field while ignoring a concurrent sequence of characters in the opposite half-field. These two-character sequences were each superimposed upon a small square background that was flickered at a rate of 8.6 Hz in one half-field and 12 Hz in the other half-field. The amplitude of the frequency-coded SSVEP elicited by either of the task-irrelevant flickering backgrounds was significantly enlarged when attention was focused upon the character sequence at the same location. This amplitude enhancement with attention was most prominent over occipital-temporal scalp areas of the right cerebral hemisphere regardless of the visual field of stimulation. These findings indicate that the SSVEP reflects an enhancement of neural responses to all stimuli that fall within the "spotlight" of spatial attention, whether or not the stimuli are task-relevant. Recordings of the SSVEP provide a new approach for studying the neural mechanisms and functional properties of selective attention to multi-element visual displays.

The brain mechanisms of visual selective attention have been studied extensively in humans by means of noninvasive recordings of transient visual evoked potentials (VEPs) that reveal spatio-temporal patterns of neural activity in cortical sensory areas (1, 2). In the case of visual-spatial attention, stimuli presented to an attended location in the visual fields elicit enhanced VEP amplitudes in extrastriate visual cortex during the interval 80-200 ms poststimulus (1, 3-5). This early enhancement of evoked cortical activity supports the hypothesis that attention to location produces an amplification of sensory information arising from stimuli within the central focus or "spotlight" of spatial attention (6).

Although a good deal has been learned about the brain's sensory systems through recordings of transient evoked potentials to individual stimuli, this approach has intrinsic limitations for investigating processes of visual attention. One major constraint is that transient VEPs are elicited optimally by stimuli having abrupt onsets that are presented at fairly long intervals (typically 0.3-1.5 s). When stimuli having these properties are used in attention experiments, however, it becomes difficult to maintain a state of focused attention upon relevant stimuli and to ignore irrelevant stimuli (7).

An alternative approach that may circumvent this limitation is to record the steady-state visual evoked potential (SSVEP) in response to a visual stimulus that is repeated at a steady rate of 8-10 Hz or more (e.g., a flickering light). The SSVEP elicited in visual cortical areas by such a repetitive flicker can be recorded from the scalp as a nearly sinusoidal oscillatory response having the same fundamental frequency as the driving stimulus (8). The amplitude and phase of the SSVEP

are highly sensitive to stimulus parameters such as flicker frequency, contrast or modulation depth, and spatial frequency (8). By recording the SSVEP to attended and unattended stimuli that are made to flicker, it may be possible to study cortical activation patterns associated with attention to stimuli that are continuously present (albeit flickered) rather than only flashed infrequently. Moreover, the SSVEP provides a continuously available signal that is readily quantifiable in the frequency domain and can be extracted from background electroencephalogram noise more rapidly than can the transient evoked potential (8, 9).

Only a few previous studies have examined changes in the SSVEP as a function of cognitive variables (9–12). In a vigilance task, Silberstein et al. (11) found that the SSVEP to an irrelevant 13-Hz flickering background was reduced in amplitude over parieto-occipital scalp areas during a period of active target detection as compared to when no target was expected. This effect was interpreted in line with the authors' hypothesis that the SSVEP to an irrelevant probe stimulus would be reduced in brain areas that are actively engaged in task-related cognitive processing (9).

These previous studies were not designed specifically to examine the effects of selective attention on the SSVEP. Such a test would necessitate an experimental design that presents two or more types of stimuli concurrently and/or unpredictably and requires the subject to attend to each stimulus class in turn on different trials (13). A study having such a design (but using auditory stimuli) failed to find any modulation of the steady-state auditory evoked potential as a function of directing attention to sounds in one ear or the other (14).

The present study is an initial attempt to test the sensitivity of the SSVEP to selective visual attention. The attentional task required subjects to attend on each trial to one of two randomized sequences of alphanumeric characters presented concurrently to the left and right visual fields, respectively. Each letter sequence was superimposed on a small background square that was flickered (8.6 Hz in one visual field, 12 Hz in the other) so as to generate SSVEPs that would reflect the selective focusing of attention on one stimulus location or the other.

METHODS

Sixteen undergraduate students (nine males, seven females) served as paid volunteer subjects in this experiment. All subjects were right-handed and had normal or corrected-to-normal vision. The data from four of these subjects (three males) were subsequently omitted from analysis because of their failure to maintain eye fixation (see below).

During testing the subject was seated 60 cm from a video monitor and was instructed to maintain visual fixation on a central cross whenever it appeared on the screen. On each trial a centrally presented arrow cue directed the subject to attend

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Abbreviations: SSVEP, steady-state visual evoked potential; EOG, electrooculogram; VEP, visual evoked potential; AI, attentional index.

to an alphanumeric character sequence (consisting of randomized presentations of the letters A through K and the number 5) in either the left or right visual field. Subjects were instructed to respond with a key press each time an infrequent target ("5") was detected in the attended sequence; target probability was 0.08 per character. The concurrent sequence in the opposite field was to be ignored. Responding hand was counterbalanced across subjects and experimental runs.

Each sequence consisted of black characters (1.0 degrees in height) superimposed upon a filled white square (2.0×2.0 degrees, 8.9 candelas (cd)/m²) (see Fig. 1). The background of the video screen was dark (0.1 cd/m²). The left and right field squares were situated on the horizontal meridian with medial edges 5.7 degrees lateral to fixation. The characters were presented simultaneously at the right and left positions for 200-ms durations with no gaps between them; each visual field received a different randomized sequence. As the characters were being presented, the white background squares were flickered on and off at a rate of 12 Hz in one visual field and 8.6 Hz in the other.

Each trial began with the onset of a central fixation cross that remained on the screen for the entire trial, and the word "Ready," which lasted for 2.0 s. Three seconds after the offset of the "Ready" signal, either a left- or right-pointing arrow was presented centrally for 1.5 s, indicating the field to which the subject should attend on that trial. The character sequences in the left and right fields and the flickering of the background squares began simultaneously 0.5 s after arrow offset and continued for 10 s. The next trial began after a 2.0-s delay.

There were four types of trials defined by the orthogonal factors of direction of attention (left or right arrow) and background flicker location (12 Hz left/8.6 Hz right or 12 Hz right/8.6 Hz left). These four conditions were presented in counterbalanced order so that each block of eight trials included two trials of each type. Each subject was tested in a total of 15 blocks.

Brain electrical activity was recorded from 13 scalp sites using tin electrodes mounted in an elastic cap. Sites included frontal (F3, F4), central (C3, C4), parietal (P3, P4), occipital (O1, O2), and temporal (T5 and T6) placements of the International 10-20 System, occipito–temporal sites (PO7, PO8) (15), and the left mastoid. Eye movements were monitored via bipolar recording of the horizontal electrooculogram (EOG) from electrodes placed at the left and right external canthi and monopolar recording of the vertical EOG from an electrode beneath the left eye. All recordings were referenced to the right mastoid except for the horizontal EOG. Electrode impedances were kept below 5 k Ω . The bandpass of the EOG recordings was 0.01-100 Hz and that of the scalp electrical recordings was 0.3-100 Hz. All data were digitized at 250 Hz and stored on disk.

Time-domain averages of the SSVEP were calculated offline over an II.0-s epoch that began 1.0 s before the start of the flickering stimuli. Separate averages were obtained for each combination of flicker frequency location and direction of attention, for a total of four averages per subject at each scalp site. High frequency noise was attenuated by digital filtering (-3-dB power at 24 Hz) of the averaged SSVEP waveforms, which were digitally re-referenced to averaged mastoids.

To rule out the possibility of differential lateral eye movements during attend-left and attend-right trials, the horizontal EOG was inspected off-line, and trials with detectable ocular deflections (about 30% of the trials overall) were rejected. The horizontal EOG was also averaged separately over attend-left and attend-right trials, and the data from four subjects who showed systematic residual EOG deviations corresponding to eye movements of 0.5 degrees or more were rejected from further analysis. For the 12 remaining subjects, the averaged EOGs indicated that the eye deviation from fixation averaged <0.3 degrees. Significantly, there was no correlation between

the size of a subject's residual eye movement and the magnitude of the SSVEP attention effect (r = -0.06; not significant).

The magnitude of 8.6- and 12-Hz SSVEP activity was quantified in the frequency domain by multiplying each averaged waveform by sine and cosine functions at the corresponding frequency, taking the square root of the sum of the squares of these two numbers, and scaling the resultant value to microvolts. This procedure was applied to the averaged waveforms in a window between 0.58 and 9.92 s after the start of the flickering stimuli to avoid any initial transient-evoked responses and to include an integral number of both 8.6- and 12-Hz cycles in the measurement window, thereby minimizing spectral leakage (16). SSVEP amplitudes were subjected to a repeated-measure analysis of variance that included the following factors: condition (attended versus unattended), side of stimulus presentation (left versus right), hemisphere of recording (left versus right), scalp site within the hemisphere (F3/4, C3/4, P3/4, 01/2, PO7/8, and T5/6), and subject. The Greenhouse-Geisser adjustment for nonsphericity was applied whenever appropriate (17).

RESULTS

Across subjects, the mean percent correct target detections was 63% (SE = 4.8%), where a correct detection was defined as a button press within a 200- to 1200-ms interval following target onset. False alarm rates were negligible.

Figure 1 shows representative SSVEP waveforms from one subject during the condition in which the 12-Hz background flicker was presented in the left visual field and the 8.6-Hz flicker in the right visual field. Recordings shown are from the right occipito—temporal scalp site (PO8) where consistent attention effects on SSVEPs were observed at both frequencies. The amplitude of the SSVEP elicited by the 12-Hz flicker was much larger in amplitude when attention was directed to the character sequence in the left visual field than to the right visual field (Fig. 1B Left), whereas the SSVEP to the concurrently presented 8.6 Hz flicker showed the reverse (Fig. 1B Right). This enhancement of the SSVEP to the irrelevant background flicker at the attended relative to the unattended location was also evident in frequency domain amplitude measures of these waveforms (Fig. 1C).

Representative SSVEP waveforms recorded at all the scalp sites from a different subject are shown in Figs. 2 and 3. The enhancement of the SSVEP to the 12-Hz flicker in the left visual field on attend-left trials was largest at occipital-temporal scalp areas over the right cerebral hemisphere (Fig. 2). In contrast, the enlargement of the SSVEP to the 8.6-Hz flicker on attend-right trials was distributed more broadly across the scalp, including substantial attention effects at anterior scalp sites (Fig. 3). Similar patterns of attention effects were evident in the group mean amplitudes (Figs. 4 and 5).

Analysis of variance of group data combined over both stimulus conditions (i.e., 8.6 Hz left/12 Hz right and 12 Hz left/8.6 Hz right) confirmed the reliability of these patterns. Overall SSVEP amplitudes were significantly enhanced by attention for both the 12 Hz (F = 7.0, P < 0.03) and 8.6 Hz (F= 8.42, P < 0.02) responses; this enhancement interacted significantly with scalp site for the 12 Hz (F = 3.91, P < 0.02) but not for the 8.6 Hz (F = 1.26, not significant) response. The posterior, right hemispheric predominance of the 12-Hz enhancement was reflected in significant interaction of attention \times hemisphere \times scalp site (F = 4.19, P < 0.02), but this interaction only approached significance (F = 2.25, P < 0.12) for the 8.6-Hz response. Interestingly, while the overall SSVEP amplitudes (collapsed over attended and unattended conditions) were greater over scalp sites contralateral to the visual field of stimulation (visual field \times hemisphere: F = 9.41, P <0.02 for 12 Hz; F = 14.05, P < 0.005 for 8.6 Hz), the attentional enhancement of these SSVEPs was not contralaterally distrib-

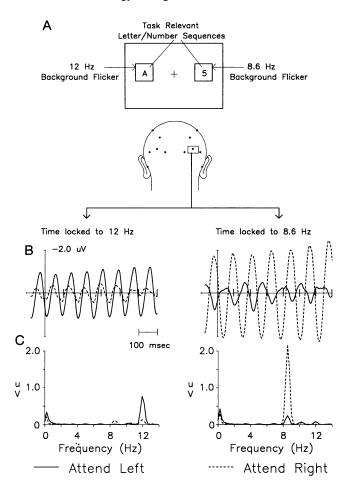


Fig. 1. Overview of experimental paradigm and results. (A) Subjects monitored the character sequence in one visual field while ignoring the contralateral sequence. In the condition shown, square backgrounds were flickered at 12 Hz in the left field and 8.6 Hz in the right. (B). Time domain averages of SSVEPs to flickering squares in the left (12 Hz) or right (8.6 Hz) visual field recorded from the right occipito-temporal scalp (site P08) in subject C.R. Waveforms shown were obtained by averaging the responses to successive flashes over the first 6 s of the flickering sequence, time locked to either the 12- or the 8.6-Hz flashes, and then averaging across all the trials of that type. Averaging epoch was 4.0 s, of which the first 700 ms is shown. Dashed waveforms correspond to Attend left condition and solid waveforms to Attend Right condition. (C). Frequency domain analysis of the SSVEPs illustrated in B. Amplitude values were derived from fast-Fourier transforms using a Blackman-Harris window (16).

uted (attention \times visual field \times hemisphere: F = 0.36, not significant for 12 Hz; F = 0.01, not significant for 8.6 Hz).

Large attentional modulations of the SSVEP were observed at the right occipito-temporal scalp sites for both flicker frequencies, although there was considerable variability among individuals in the magnitude of this effect. Whereas some subjects showed a 3- to 4-fold increment in SSVEP amplitudes with attention, others showed little or no change. In terms of percentage enhancement (attended relative to unattended amplitude), the magnitude of the attention effect over the right hemisphere (PO8 and T6 sites) averaged 77% (SE = 26%) for the 12-Hz and 108% (SE = 59%) for the 8.6-Hz response. Nine of the 12 subjects showed overall SSVEP enhancements of >50%.

These attention effects on SSVEP amplitude were also quantified in terms of an attentional index (AI), calculated as follows: AI = (attended amplitude - unattended amplitude) \div 1/2 (attended amplitude + unattended amplitude). These AI values at the PO8 and T6 sites averaged together were significantly greater than zero for both the 12-Hz (AI = 0.46,

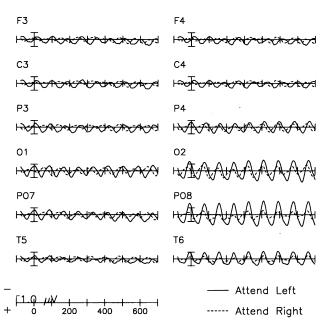


Fig. 2. Time domain averages from subject H.E. of the SSVEP elicited by the 12-Hz flicker presented in the left field. Recordings are shown from 12 scalp sites, all referenced to averaged mastoids. Attending to the location of the 12-Hz flicker produced a marked amplitude enhancement in the right occipito-temporal region (sites O2, PO8, and T6).

F = 26.03, P < 0.0003) and 8.6-Hz (AI = 0.45, F = 1.41, P <0.01) responses. The right hemispheric lateralization of this attention effect was tested by comparing the AIs at right (PO8/T6) versus left (PO7/T5) hemispheric sites; this comparison was significant for the 12-Hz response (F = 8.14, P <0.02) but not for the 8.6-Hz response (F = 1.82, not significant).

As can be seen in Figs. 1-3, spatial attention could affect SSVEP phase as well as amplitude, but the pattern of phase changes at different scalp sites varied among individuals. These complex attention effects on SSVEP phase and the possible

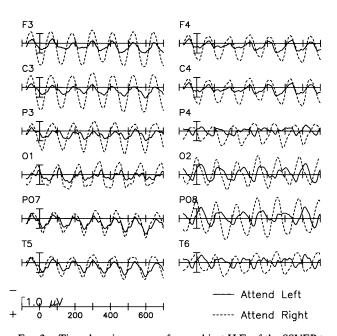


Fig. 3. Time domain averages from subject H.E. of the SSVEP to the 8.6-Hz flicker presented to the right stimulus location, recorded concurrently with the 12-Hz SSVEP shown in Fig. 2.

FIG. 4. Mean SSVEP amplitudes over all subjects calculated in the frequency domain in response to the 12-Hz flicking background. Total bar height represents the mean attended amplitude at each scalp site, and shaded bar height represents mean unattended amplitude. Vertical lines give standard errors. Amplitudes are averaged over conditions of left and right field of stimulation.

effects of phase variability on amplitude measures are beyond the scope of this report.

DISCUSSION

The SSVEP was found to be strongly modulated by spatial selective attention, being substantially enlarged in response to a flickering stimulus at an attended versus an unattended location. This modulation occurred even though the background flicker was irrelevant to the assigned task of attending to the superimposed sequence of letters and numbers. This suggests that the increased SSVEP amplitudes reflect an enhancement of neural responses to all stimuli that fall within the spotlight of spatial attention, whether or not they are task-relevant. These attention effects on irrelevant probe stimuli support a mechanism of early stimulus selection based solely on location (18).

The attentional modulation of the SSVEP was generally larger over the right cerebral hemisphere as compared to the left, particularly for the 12-Hz response. This laterality effect

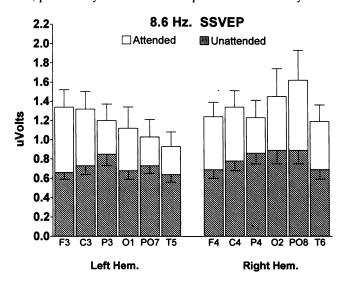


Fig. 5. Mean SSVEP amplitudes over all subjects to the 8.6-Hz flickering background, depicted as in Fig. 4.

fits in with accumulating evidence that the right hemisphere plays a predominant role in spatial attention (19). In contrast, attentional enhancement of the transient VEP has been found to occur primarily over the hemisphere contralateral to the field of stimulation for some components and over the ipsilateral hemisphere for others (1, 3–5). This difference in the localization of transient and steady-state attention effects suggests that they are indices of different aspects of spatial selection mechanisms.

The present results may be compared with those of Silberstein et al. (11), who recorded the SSVEP to a large diffuse background flicker during a visual vigilance task. In that study, it was found that SSVEP amplitude actually decreased during a period of active vigilance in relation to a period of passive viewing. This contrasts with the present finding of an increase in SSVEP amplitude to attended-field stimuli. The apparent conflict between the two studies might be attributable to differences in the relative sizes of the flickering background and task-relevant stimuli. In the study of Silberstein et al. (11) the flickering background was very large (30 \times 80 degrees) in relation to the superimposed relevant stimuli (1 degree). Under these conditions, the narrow focusing of the attentional spotlight upon the relevant stimuli may have suppressed the SSVEP to the diffuse surrounding flicker. Another possibility is that SSVEP differences between the attend and nonattend conditions in the experiment of Silberstein et al. (11) may have been affected by changes in nonselective factors such as general arousal or alertness levels. The design of the present study, however, allows the SSVEP changes to be attributed specifically to shifts in spatial-selective attention (13).

The present findings indicate that the allocation of attention between two steadily flickering stimulus locations is reflected in the relative amplitudes of frequency-specific SSVEPs elicited by each source. This observation suggests that SSVEPs may be used to advantage in further studies of visual attention to continuously presented stimuli, which may involve sensory selection mechanisms different from those engaged during attention to transient stimulus onsets or offsets. The present results further suggest that the neural generators responsible for the SSVEP are different (at least in laterality) from those manifested by the transient VEP, and the underlying brain systems can be further differentiated in future studies using source localization techniques.

The SSVEP also appears well suited to studying the spatial and temporal properties of attentional focusing within a visual display, since it is rapidly quantifiable with a high signal-to-noise ratio (8). Thus, it may provide an on-line measure of the shifting of attention among different elements of a display and may allow tracking of the onset and rise-time of attentional switching. Furthermore, because the SSVEP can be elicited by an irrelevant background flicker, it can be used to study spatial attention to any type of superimposed stimulus, whether it be a rapid pattern sequence as in the present study or a stimulus that shows little or no change over time. In the latter case, the SSVEP may have practical applications for monitoring an observer's state of attention and alertness over an extended period of time.

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